VISUAL ORIENTATION AT THE WATER SURFACE BY THE TELEOST *ZENARCHOPTERUS* [1]

RICHARD B. FORWARD, JR.,[2] KENNETH W. HORCH [3]
AND TALBOT H. WATERMAN

Biology Department, Yale University, New Haven, Connecticut 06520

In seeking quantitative documentation that certain teleosts can perceive the *e*-vector of linearly polarized light (earlier work reviewed in Waterman, 1972), a number of field experiments have been carried out on the viviparous tropical half-beak *Zenarchopterus* (Hemirhamphidae). Most of these were underwater studies conducted with single fish enclosed in a covered transparent vessel and exposed to various illumination patterns including both natural and imposed polarized light (Waterman and Forward, 1970; 1972).

Although halfbeaks were behaviorally responsive in this submerged situation, they normally swim at the water surface. In order to include this potentially important feature of the fish's visual and tactile environment, additional experiments were conducted on land with the fish swimming in an open experimental vessel. Under such conditions a fairly vigorous basic polarotaxis was evoked that was somewhat different from that previously observed. Also new evidence was found relating to other components in the fish's visual orientation. These studies of *Zenarchopterus'* visually evoked directional behavior at the water-air interface are the subject of the present report.

To begin with some precise definitions of terms describing animal orientation to light may be helpful. *Phototaxis* is the directionally oriented response of an organism to light intensity patterns (Kuhn, 1919; Fraenkel and Gunn, 1940; Jander, 1970). The comparable response to light polarization patterns is *polarotaxis* (Waterman, 1966), *i.e.*, a directional response in relation to a given plane or pattern of polarization. When the resulting orientation (body axis alignment or steering direction of locomotion) has a fixed, non-graded angular relation to the stimulus, *e.g.*, heading toward the light (0°) or away from it (180°) (photo-taxis), or at 0°, 45°, 90°, 135° to the *e*-vector (polarotaxis), then it may also be called a "basic" response or *basitaxis* (= "basotaxis" of Jander, 1963a, 1963b).

In contrast to basitaxis there is another relatively simple type of response to spatial differences in light intensity. This is *photomenotaxis*, or the light compass reaction (von Buddenbrock, 1917), in which orientation may be at *any* temporarily fixed angle to the stimulus source. A comparable compass orientation depending on linearly polarized light is also well known in many arthropods (Waterman, 1966).

For behaviorally significant direction-finding which utilizes celestial cues, a menotaxis rather than a basitaxis would ordinarily be needed, since the course

[2] Present Address: Duke University Marine Laboratory, Beaufort, North Carolina 28516.

[3] Present Address: Department of Physiology, University of Utah, Salt Lake City, Utah 84112.

heading required would depend on the animal's present position relative to the location of its "goal." Thus as the animal moves the angular relationship between the compass direction connecting these two points and the reference cue will usually vary with time. Moreover, if the orientation is to be accurately maintained by celestial reference for more than a few minutes, the compass reaction would have to be time compensated to allow for the apparent movement of the sky and celestial bodies as the earth rotates (von Frisch, 1950; Kramer, 1950).

Fishes have been shown to be capable of a *time-compensated sun compass orientation* (reviews: Hasler, 1966; Harden Jones, 1968; Waterman, 1972). This ability implies that from their underwater vantage point fishes are able to determine the sun's azimuth direction and possibly its altitude. Close to the surface and in a flat calm this might be accomplished by direct observation of the sun's disc or sky polarization. Otherwise it could be derived either from the radiance distribution in the water or from the underwater polarization pattern, both of which are directly dependent on the sun's position (Waterman, 1954; Jerlov, 1968; Lundgren, 1971).

The light intensity distribution is probably suitable for accurate localization (within say 6°) in shallow water (5–10 m). However, the useful information from this radiance pattern decreases rapidly with increasing depth (Harden Jones, 1968). A more precise indicator of the sun's position which penetrates to greater depths is the polarization pattern underwater (Waterman, 1955; Ivanoff and Waterman, 1958). Therefore, demonstration of polarotaxis by fish would imply that they are capable of perceiving this component of natural submarine illumination. In turn this suggests that they could use the underwater polarization pattern to localize the sun.

We present herewith new evidence for polarotaxis as well as for time compensated sun compass orientation by the fish *Zenarchopterus*.

EXPERIMENTAL METHODS

The experiments were carried out in Palau, Western Caroline Islands (U. S. Trust Territory of the Pacific Islands) on August 28th and 29th, 1970. The general methods employed resemble those for the corresponding underwater studies (Waterman and Forward, 1972) except that the fish were tested in a transparent vessel open to the air with a free water surface.

The experimental site was the broad cement apron of an abandoned seaplane ramp on the north shore of Arakabesan Island (*E*, Fig. 1). Single fish were placed in a cylindrical transparent plastic container, 19 cm in diameter and 7.5 cm deep. The vessel was positioned above an intervalometer-controlled Robot camera, and screened laterally and downward by white, cylindrical screens and a diaphragm. Thus, the fish had a free view of the sky through the water surface, but was prevented from seeing surrounding landmarks, the experimenters or the equipment (except for the camera lens). To minimize reflection from the meniscus or from the cylinder's plastic wall in air, the vessel was carefully filled with seawater just to its brim. Freshly caught, experimentally naive juvenile *Zenarchopterus dispar* (Cuvier and Valenciennes) 40–50 mm in length were used. All fish were collected at a localized site on Auluptagel Island (*H*, Fig. 1).

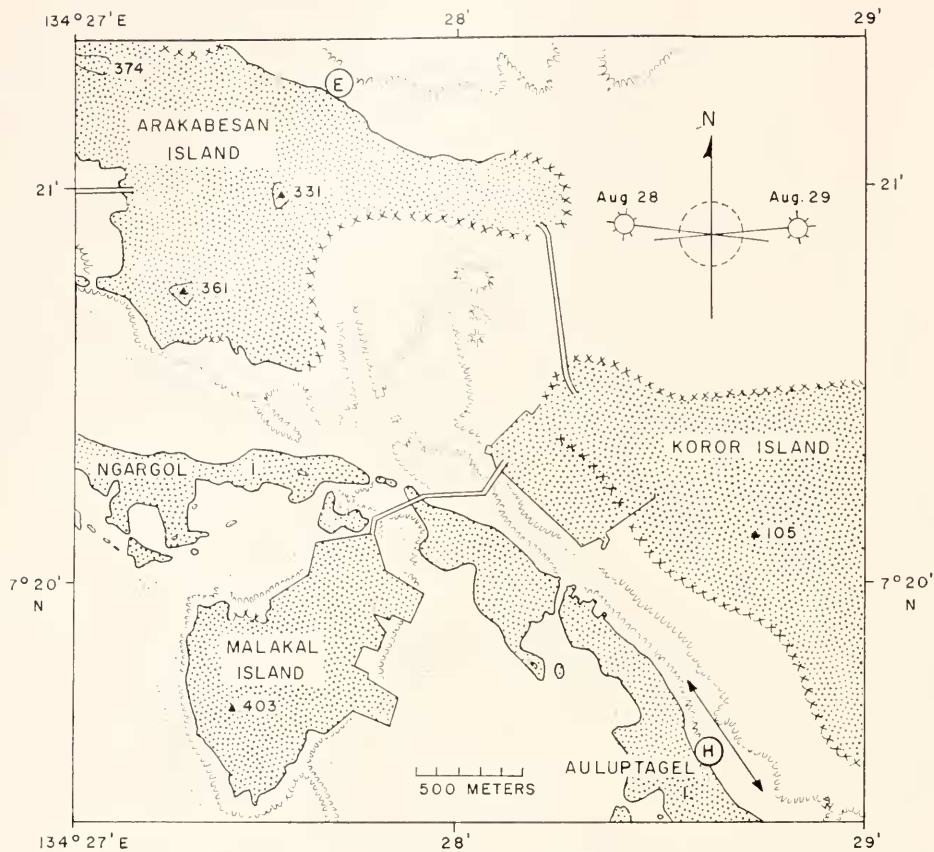During the experimental period, the sun's bearing and elevation were deter-

FIGURE 1. Map of Arakabesan, Auluptagel, and nearby area of the Palau Islands. The experimental site was at *E* and all the *Zenarchopterus* used were collected at *H*. The double headed arrow near the latter indicates the main trend of the inter-island channel adjacent to *H* (channel axis 150–330°). Island peak elevations are given in feet. Outer edge of coral reefs are represented by scalloped outlines, mangrove areas by cross-hatching.

mined every 10 min with compass and sextant (Fig. 2). To document cloud cover conditions, photographs of the sky were taken at similar intervals with a camera having a fisheye lens. The sky generally was 35–40% obscured by light scattered clouds on the two days concerned. However, fish orientation was recorded only when the sun was clearly visible. When a small cloud briefly obscured the sun, measurements were suspended until the sun was again shining.

Twenty-four specimens of *Zenarchopterus* were studied, each under four optical conditions: (1) without the polarizer (NF condition), during which the fish was exposed only to the natural illumination of sun and sky; and (2, 3 and 4) with a Polaroid linear polarizer (Type KN36) placed over the experimental vessel (WP condition) and oriented at three different directions with respect to the sun's bearing (Fig. 3). Since six planes of polarization were tested altogether (0–180°, 30–210°,

60–240°, 90–270°, 120–300°, 150–330°), only half were used with an individual fish.

For each condition, 10 consecutive photographs of the fish's headings were made at 10 sec intervals timed and counted by the intervalometer. The filter was then changed manually to its next position or removed for the NF condition. After a 10 sec pause to let the fish settle down, another 10 frame sequence was made, etc. The order of presentation of the conditions, as well as the angle of the polarizer were randomly selected with the constraints that no condition was used twice with a given fish, and all conditions were tested an equal number of times.

The angle between the fish's longitudinal axis and the sun's bearing taken as 0° reference was measured to the nearest 10° from the photographs. For analysis these headings were grouped into 30° sectors centered to coincide with the six
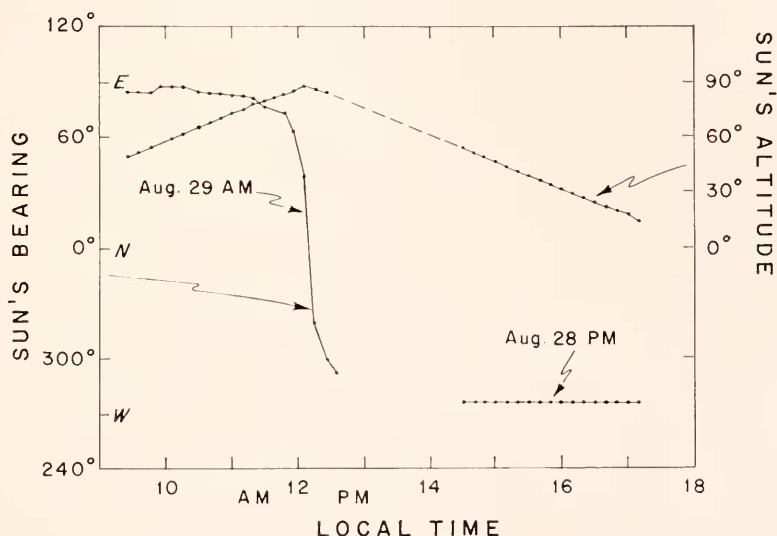

FIGURE 2. Sun's bearing and altitude during the experimental periods. Note that for August 28th the solar bearing was constant near W by WNW during the full period. On the 29th the bearing was stable for the first 2.5 hours, then it shifted very rapidly. For this reason measurements made during the last 30 min (4 of the 12 fish) were excluded from the main analysis.

polarization planes tested. Obviously the positions and angular extent of these sectors are fixed and the response variable is the number or percentage of observed orientations which falls within each.

The experimental design permits the overall data to be analyzed in several ways to test for various significant stimulus components. Thus the total distribution as recorded has the sun's bearing at 0° and the imposed e-vector randomized (Fig. 3). When transposed to geographical coordinates (0° = North) the e-vector is still at random but the sun's bearing appears mainly in two opposite directions. Their effect can be determined by separating the data for days.

The NF data can be compared with the randomized WP distribution to check for possible behavioral changes due to other features of the polarizer than its e-

vector orientation. Then the WP counts can be transposed so that all the imposed e-vectors are aligned with the 0°–180° plotting axis. This distributes the influence of the sun and any geographically derived effects leaving just polarotaxis as the predominant source of orientation in the resulting pattern. Finally the NF data can be compared with those for any particular imposed e-vector orientation.

To begin with the responses of the 24 individual fishes were studied in detail. Previous experience showed that "inattentive" fish significantly decrease the overall response level to potential orienting stimuli (Waterman and Forward, 1972). Obviously a completely inactive fish and one orienting consistently "on the beam" will both maintain constant headings. However, the inattentive animal can be recognized by its failure to change headings over a long period even when the
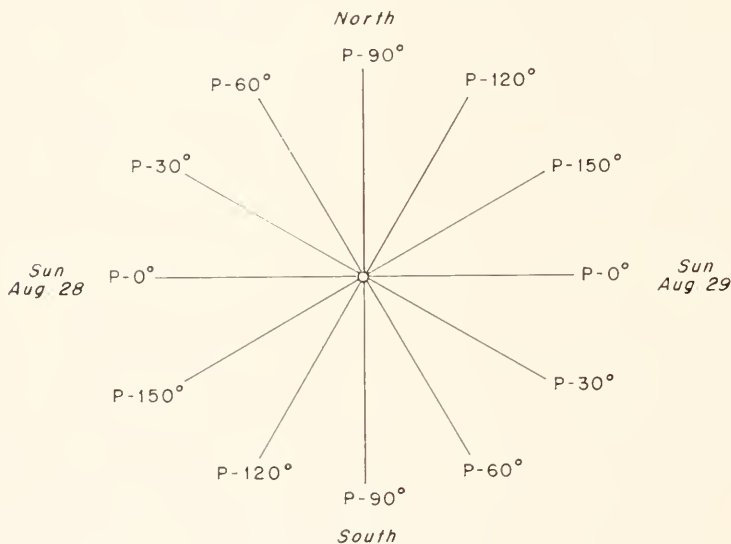

FIGURE 3. Angular relationship between North, sun's azimuth and polarizer e-vector directions (P-0°, etc.).

experimental conditions are altered. Inattention may also appear as a continuously changing orientation at a constant or high velocity. In such cases no externally cued directional preferences may be involved.

The major results presented below are derived from data selected to minimize these difficulties. However, the effects of such selection have been repeatedly checked by comparisons with the total data and with distributions resulting from alternative selective procedures. For example the last four fish run on August 29 were eliminated from prime consideration because the sun was changing its bearing very rapidly during their runs (Fig. 2). Also at that time the solar zenith distance, and hence the sun's potential influence in determining azimuth, was minimal as was the sky polarization near the zenith.

Indeed these fish showed different but less coherent orientation preferences than those run with steady sun's bearings. Nevertheless addition of their counts

to those of the other 18 orienting fish does not alter the location of significant sectors relative to the North, sun, or *e*-vector. Nor do they significantly affect the overall NF distribution.

Furthermore two other fish from the afternoon sequence were eliminated from the selected data because they scarcely changed their headings throughout the set of four conditions tested for each. Hence 18 of the total 24 fish provide the orientation headings analyzed in most detail.

Moreover for all fish rather large angular changes of direction sometimes did occur between frames. To decrease the influence of such more rapid turning, we have for our selected data rejected orientation measurements which differed from their predecessor by more than 20°. The remaining headings are interpreted as "pauses" in directions preferred by the fish and possibly determined by some external clue for azimuth.

Since behavior patterns of the individual fish were different the number of pauses observed under each experimental condition varied. Therefore, to prevent over or under representation by any one condition when totaling the results, the data for each condition were converted into percentage responses in each 30° sector. Where different conditions are combined, the percentage responses in each angular category are totaled and divided by the number of conditions used.

Ninety-nine per cent binomial confidence limits were computed for the observed frequency of responses in each sector. If the expected frequency for a uniform distribution (*e.g.*, 8.3% in each 30° sector of a circle) fell within these limits, the observed frequency is considered not significantly different (at the 1% level) from a random, non-oriented response. Otherwise, it is indicated in the figures as being above (plus sign) or below (minus sign) the expected value.

Note that this treatment was used instead of the attractive circular normal method (Batschelet, 1965; Waterman and Forward, 1970) because our data are generally not the normal, unimodal, continuous distributions appropriate to the latter. Furthermore most of our comparisons are made with normalized relative frequencies, not with the actual counts.

Results

For all 24 fish on the two days 933 heading counts are available including all seven conditions; the corresponding number for the pauses, as defined above, is 636. For the 18 selected fish which were orienting while the sun's bearing was steady the total data are 775, the pauses 444. Consider first the circular distribution of the 18 fish on two days summed for all conditions (WP and NF) and plotted relative to North (Fig. 4A). Here all three sectors in the southerly quadrant are significantly preferred as is the sector centered at 30°.

Examination of the detailed data shows that the last sector's significance depends mainly on several runs on the afternoon of August 28. The pause criterion eliminates these counts, however, while reinforcing the southward preference (Fig. 4B). Indeed the pause count in the 30° sector in Figure 4B is significantly less than expected as are those in the other sectors from North to West. We can conclude then that the peak near NNE is behaviorally distinct as it is associated with more rapid turning by the halfbeaks. The broad southerly preference is characteristic of both the total counts and the pauses.
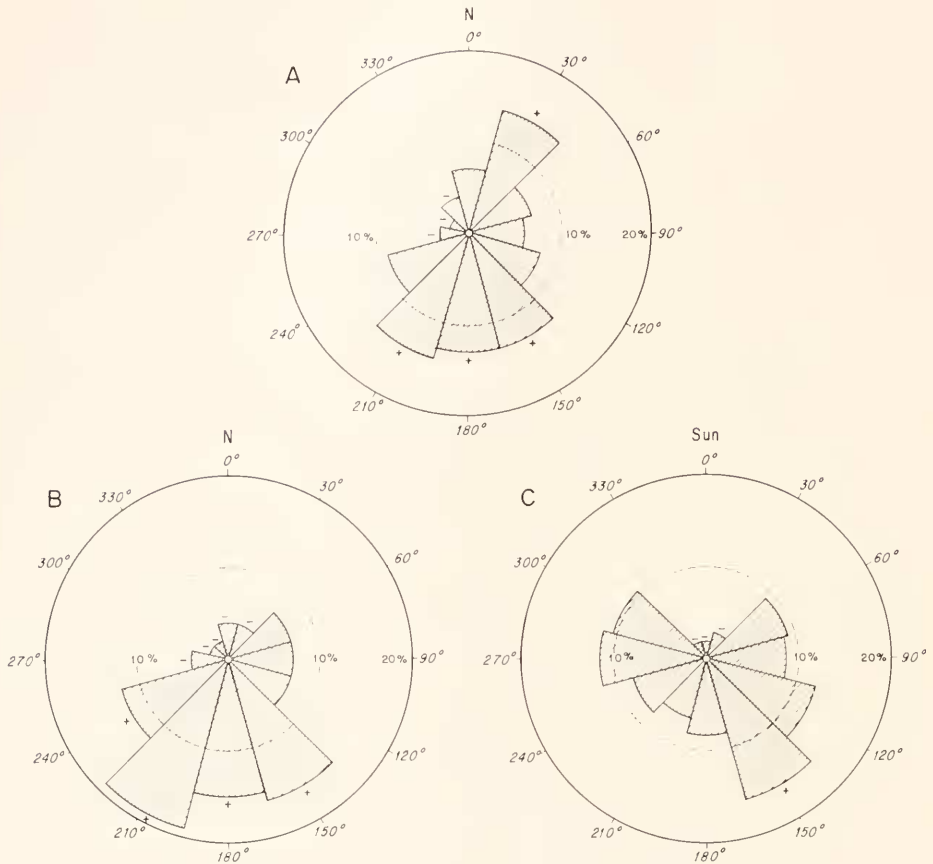
FIGURE 4. *Zenarchopterus'* directional responses relative to North and to the sun. A and B permit comparison of total (n = 775) and pause (n = 444) data (see text for definitions) plotted relative to North at 0°. B and C (n = 444) compare the pause data distributions relative respectively to North and to the sun's bearing. Eighteen fish, both days, seven conditions (one without polarizer and six different *e*-vector directions). Plotted as percentages of the numbers observed in twelve 30° sectors around 360°. Directions whose sectors contain greater percentages than expected at the 99% confidence level are indicated by "+" and those having less than expected by "−." The distribution in Figure 4C is dissected by days in Figure 5.

To analyze this geographic directional choice further the data need to be considered relative to the sun's bearing. When so plotted the pause distribution obtained for the 18 selected fish shows only one significant preferred sector at 150° clockwise from the sun's bearing (Fig. 4C). However, note that the whole quadrant centered in the solar direction is significantly avoided.

Since the sun's bearing differed by nearly 180° on the two experimental days (Fig. 2) this overall distribution needs to be dissected accordingly. The corresponding orientation patterns are quite different (Fig. 5A, B). Both are vertical and skewed away from the sun. But in the morning data (Fig. 5B)

the significant sectors are at 60°, 120° and 150° re the sun's bearing. Geographically these range from about SSE through SW. In contrast the afternoon data (Fig. 5A) show peaks at 240°, 270° and 300°. But their geographical distributions are about SSW, S and SSE. On both days the quadrant centered on the sun's bearing was significantly avoided as was one other quadrant which reference to the geographic coordinates identifies as northerly for each case. The apparent avoidance of the sun's general direction and the broad southward tendency which is shown by a preponderance of headings 90° to the sun's vertical indicate that the solar azimuth is involved in the observed responses.

These implications are strengthened by the oriented reactions to the NF condition where the fish were responding without a filter-imposed *e*-vector (Fig. 6A). Some counts appear in all but one sector (300° re N) but the only direction
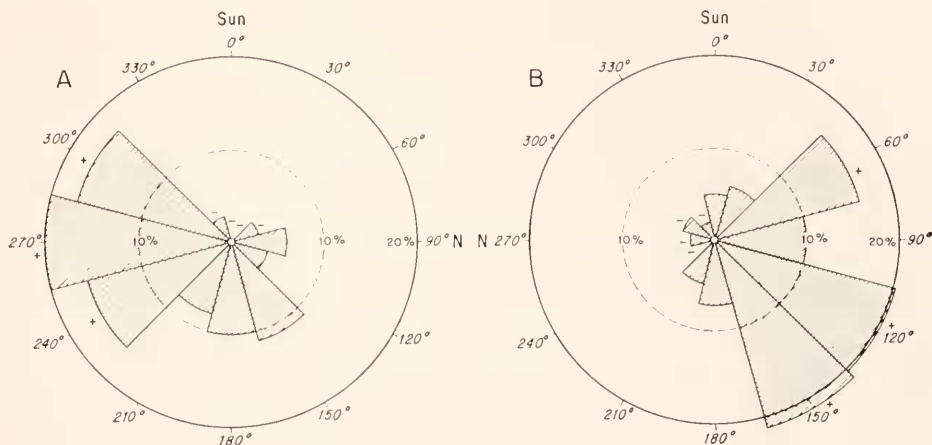

FIGURE 5. Comparison of *Zenarchopterus'* orientation relative to the sun on the two experimental days; (A.) August 28, 10 fish, n = 253; (B.) August 29, 8 fish, n = 191; pauses only, seven conditions (one without polarizer, six with different *e*-vector directions). Sectors and significant directions as in Figure 4. Figure 4C is the sum of the data in Figures 5A and 5B.

significantly preferred was 180° (South). In addition the southerly quadrant was preferred in 45% of the pause headings. Examination of the corresponding total count distribution for the 18 fish shows a similar pattern except that an additional significant peak is present at 30°.

We have already seen that this is associated with faster turning and is eliminated by the pause criterion. The 24 fish total count distribution like the 18 fish pause count for NF has only one significant sector and that, too, is at 180°; the last four fish on the 29th reacting while the sun's bearing was changing rapidly showed no significant peaks in their NF distribution. Thus a strong southward orientation was evident in our *Zenarchopterus* data not only with the six WP conditions (randomized *e*-vector) plus NF but in the last condition alone where just the natural illumination was available.

Of course the blue sky visible in the NF condition has its own characteristic

polarization pattern. A comparison between the NF response and that WP condition most closely simulating the natural pattern should therefore be instructive. The sky polarization in the zenith and all along the vertical great circle passing through the sun, *i.e.*, the sun's vertical, is perpendicular to the solar bearing. Consequently the 90° WP condition of the six used would no doubt most closely resemble the natural sky pattern.

In the latter, however, the degree of polarization, maximum about 90° from the sun, varies for blue sky from 50–90% depending on the earth's albedo, the turbidity of the atmosphere and the sun's zenith distance (Sekera, 1957). Near the surface, if the water is relatively calm as in our experimental vessel, this polarization as
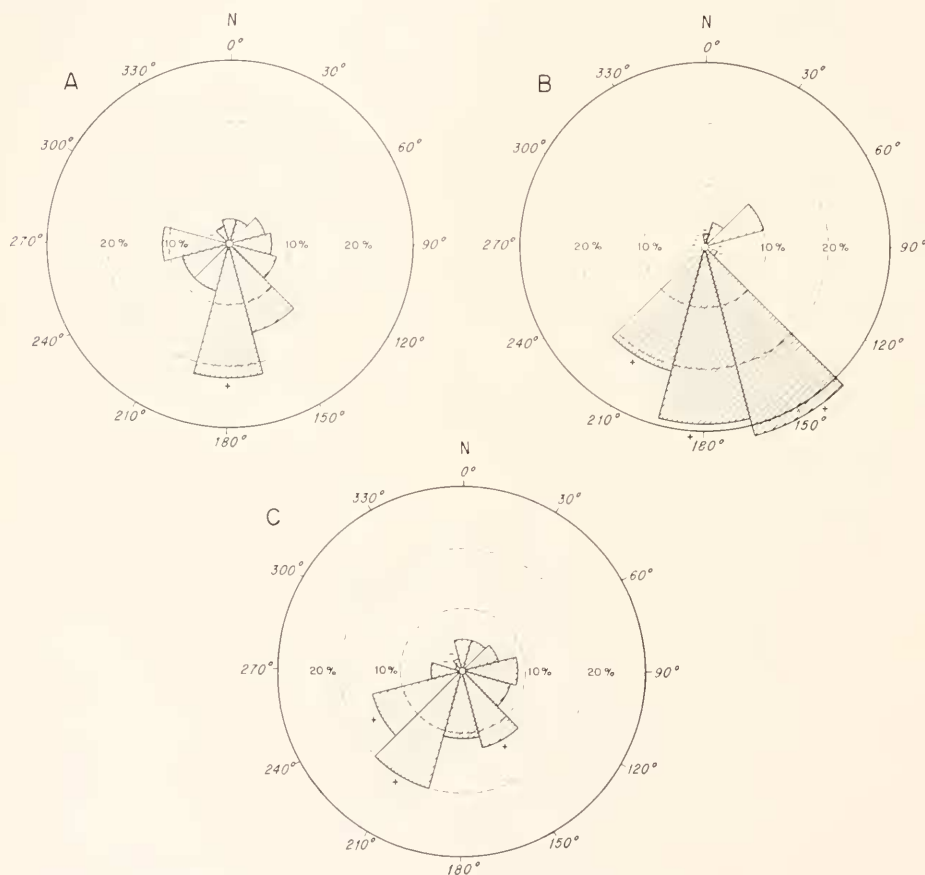

FIGURE 6. Comparison of *Zenarchopterus'* orientation relative to North under natural illumination and with different *c*-vector directions imposed by a polarizer; (A.) natural illumination without polarizer (NF condition), n = 96; (B.) with polarization plane at 90° to the sun's bearing (parallel to natural polarization in the sun's vertical), n = 53; (C.) with-polarizer runs for five of the six specific *c*-vector directions (WP at 0°, 30°, 60°, 120°, 150°). Note that WP 90° (Fig. 6B) is excluded here. See text for discussion, n = 295; Eighteen fish, pauses only. Sectors and significant directons as in Figure 4.

well as that of the whole sky would be directly observed underwater through the critical angle (Waterman, 1954). In contrast our experimental 90° WP condition provided nearly 100% polarization of the visible light with the *e*-vector perpendicular to the sun's bearing apparent through the whole sky not just along the sun's vertical.

The corresponding halfbeak orientation with 90° WP indicates that more than half of the sectors were avoided and the three southward ones (approximately SSE, S and SSW) were significantly preferred at better than the 1% level (Fig. 6B). Indeed 82% of the headings in this distribution fall within the southerly quadrant.

Note that the approximately 65% reduction in luminous flux due to placing the polarizer over the experimental vessel did not alter the fishes' general behavior or azimuth preference when the imposed *e*-vector was parallel to that of the sky in the sun's vertical. Actually the resulting increases in the degree of polarization and the extension over the whole celestial hemisphere of the N-S *e*-vector direction naturally present in the sun's vertical are correlated with a reinforcement of the southward preference.

Because rather similar strong southerly preferences were demonstrated by the NF and 90° WP data one could argue that these two conditions (out of the seven tested) were sufficient to dominate the overall data distribution relative to geographical North (Fig. 4A, B). This is not the case, however. If all the pause data minus the NF and 90° runs are plotted, 44% of the headings are still in the quadrant centered on S (Fig. 6C). This is a significant preference over random for the four quadrants at better than the 1% level. The same was true of course for the NF and 90° WP plots themselves (Fig. 6A, B) but this tendency persists in the rest of the data, too (Fig. 6C). Therefore we can conclude unambiguously that the southward preference indicated in the total WP plus NF pauses is not due to the NF and 90° runs alone.

To test for any polarotactic effect of the imposed *e*-vector all responses to the six geographical directions of polarization plane produced by the Polaroid filter should be appropriately grouped and totaled. To permit this data were "zero corrected" by transposing counts so that the *e*-vector directions for all six WP conditions fall on the 0–180° plotting axis. Since polarized light is symmetrical about the *e*-vector axis, diametric responses, *e.g.*, 90° and 270° are equivalent (Fig. 2). Thus, if it perceives the polarization plane an organism can tell whether its anteroposterior axis is heading to the right or left of this *e*-vector. However, on the basis of that clue alone orientation would be subject to an 180° ambiguity around the horizon.

Heading responses were therefore folded around the axis perpendicular to the plane of polarization by adding diagonal pause counts. This yields a semicircular distribution counterclockwise (left) and clockwise (right) from the *e*-vector. Corrected in this way, a fairly strong and significant (at the 1% level) preference is shown for the 0° direction, *i.e.*, parallel to the *e*-vector (Fig. 7A).

The validity of this conclusion can be reinforced by showing that the selection of data for pauses sharpens the decided preference of *Zenarchopterus* for orientation parallel to the *e*-vector. Yet it does not alter the inferences which may be just as clearly drawn from the unselected total data for the 18 fish (Fig.
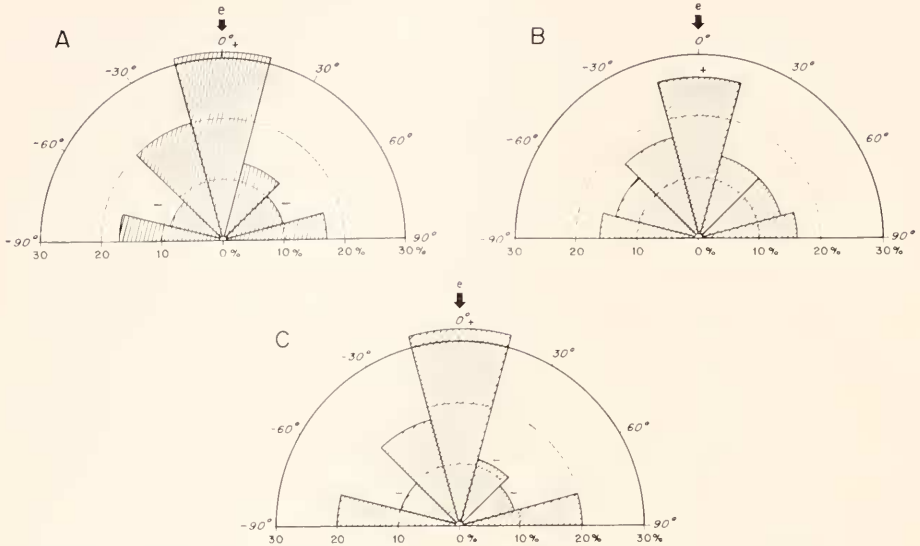
FIGURE 7. Polarotactic responses of *Zenarchopterus* to imposed linear polarization. (A.) data for all six tested *e*-vector directions (6 WP conditions) superimposed, pauses only, n = 348; (B.) same as Figure 7A but total counts used instead of just pauses, n = 578; (C.) same as Figure 7A but counts for WP 90° excluded; WP 0°, 30°, 60°, 120° and 150° included, n = 295; Eighteen fish. Sectors and significant directions similar to those of Figure 4 but data folded to 180° as described in text.

7B). There the distribution is somewhat more random, no sectors are significantly avoided and only 26% instead of 31% of the headings are parallel to the plane of polarization. Nevertheless the 0° sector is again the only one significantly preferred.

Finally we can show that the strong southerly preference of the 90° WP data (Fig. 6B) adds to but is not by any means the only support in the total WP data for orientation parallel to the *e*-vector. Thus subtracting the 90° WP headings from the overall WP distribution yields a new plot (Fig. 7C). However, its implications are exactly the same as for the selected pause data (Fig. 7A) and the total unselected headings (Fig. 7B). Again the only significantly preferred sector is that centered at 0° (Fig. 7C). This may be taken as evidence that *e*-vector direction can at least partially override orientation clues.

DISCUSSION

These results for *Zenarchopterus* demonstrate a time compensated menotaxis, a polarotaxis and, possibly, a negative phototaxis. The last is suggested by the significant avoidance of the sun's quadrant evident in distributions plotted relative to the solar bearing (Fig. 4C, Fig. 5A, B). However, in the absence of controls, other explanations of this are possible such as strong positive preference for different directions which would leave the solar quadrant relatively empty.

On the other hand the case for a time compensated menotaxis is well supported by the marked preference for southerly headings shown by the fish

(Figs. 4B, 6A, B, C). This must be time compensated because South was 90° counterclockwise from the sun on August 28 and 90° clockwise on August 29.

Preliminary observations indicated that the fishes' orientation was weak or absent when clouds obscured the sun even though only 35–40% of the sky was covered. This reinforces the conclusion supported by the heading distributions plotted relative to the sun's bearing (Figs. 4C, 5A, B) that the observed response is a *photo*menotaxis and not behavior mediated by another untested sensory modality *e.g.*, geomagnetic or geoelectric fields (McCleave, Rommel and Cathcart, 1971). In fact the relations between the response distributions obtained with the various conditions tested indicate that the preferences observed must be primarily visually determined. For example the four fish tested at the end of the August 29 sequence when the sun's bearing was changing rapidly were disoriented relative to the first eight fish run with a steady solar azimuth.

The menotactic directional preference was more precise for the 18 selected fish under natural illumination (NF) than in the totals for all conditions; for the NF distribution the only significant preference was due South at 180° (Fig. 6A). Similarly a preponderant number of headings occurred in the southerly quadrant for the 90° WP condition (Fig. 6B). Note, however, that even if these two conditions are subtracted from the total counts, the remaining data (WP at 0°, 30°, 60°, 120°, 150°) also show highly significant southward preference (Fig. 6C).

This preferred geographical direction perhaps relates either to the axis of the channel (150°–300°) at the collecting site (Fig. 1) or the direction (150° relative to North) which leads from the experimental area (E, Fig. 1) to the site of collection (H, Fig. 1). Previous underwater tests had also demonstrated menotactic preference for the directions approximately parallel to the channel of the fish's normal habitat (Waterman and Forward, 1972). More experiments are necessary to determine the validity of these several correlations.

It is not clear from the present results whether the fish are using the sun's position directly or the related sky polarization patterns to select their preferred geographical headings. The fact that *Zenarchopterus* tends to orient parallel to imposed *e*-vectors different from that in the sun's vertical (Fig. 7C) shows that they can and do orient to the plane of a superimposed polarization pattern. Also as noted above increasing the degree and area of overhead polarization having its *e*-vector parallel to that in the sun's vertical was correlated with a reinforced southerly orientation preference. This suggests but obviously does not prove that sky polarization plays a role in the responses of *Zenachopterus* to natural illumination.

However, the strong asymmetry of the present data's geographical distributions shows that more than the plane of imposed polarization must be involved. The *e*-vector is of course symmetrical through 180° and therefore by itself indicates pairs of opposite geographical directions. Perhaps there is an interaction between a polarotaxis symmetrical through 180° and a response dependent on the sun's asymmetric position.

As mentioned above the fish in preliminary experiments showed little or no orientation when the sun was obscured by clouds. A similar correlation also appeared in our underwater experiments with *Zenarchopterus* (Waterman and Forward, 1972). This finding may seem rather surprising in terms of the ex-

pectation that polarotaxis functions merely as a supplementary "sun compass" when the sun itself is obscured. However, our results may indicate instead or in addition that there is a releasing effect of the sun's disc (or the correlated high light intensity) on the underlying orientation preferences. Clearly such hypotheses must be tested by further experiments.

The strong polarotactic preference for orientation parallel to the e-vector of the downward illumination is unequivocal in these experiments. Essentially the same heading pattern appears in the data corrected to superimpose the e-vector whether the six pause distributions for different directions of the polarization plane are plotted (Fig. 7A) or the total WP data (Fig. 7B), or the pauses minus the 90° counts (Fig. 7C). Hence the observed behavior must be a polarotaxis and not just some other overriding response yielding southerly orientation.

This polarotactic orientation of *Zenarchopterus* swimming at the water surface differs in several ways from the distributions previously observed underwater (Waterman and Forward, 1972). Thus the present response to the e-vector appears considerably stronger in the total data than in the six day sequence of underwater experiments. The polarotactically preferred sector in the water surface experiments comprised 26% of the distribution (Fig. 7B) the corresponding sector in the underwater case contained only 19%.

However, in the underwater data selection of fish and using criteria for pauses increased the relative counts in the most preferred direction to 27% whereas the corresponding sector for the water surface experiments increased relatively less but reached 31% for the pauses (Fig. 7A). Consequently future experiments should most likely make use of this stronger orientation and the obvious practical advantages of the water surface type of tests. In addition the experimental situation at the water-air interface more closely mimics the environmental conditions usually experienced by this particular fish. Hence results like the present ones may be a better indicator of normal behavior.

A second difference between these and the previous experiments is that both perpendicular and parallel polarotaxis were observed underwater with the former being the more pronounced (Waterman and Forward, 1972). Only parallel polarotaxis is significantly preferred in the present results. Third, those submarine studies showed that strongest polarotaxis occurred to imposed e-vectors differing maximally in direction from that of the natural illumination in the sun's vertical (Waterman and Forward, 1972). This is not evident in the present data.

A fourth difference is that no oblique orientation to the e-vector is observed in the water surface results. In the underwater experiments the fish oriented either in the 0°, 90°, 180°, 270° quartet of directions or in one of the four oblique alternatives. Such bimodal preference patterns (parallel or perpendicular *vs.* oblique) are well known in both crustaceans and insects; corresponding four-peak preferences occur in cephalopods, too (Waterman, 1966). However, the responses of these other animals are most likely basitaxes evoked under particular experimental conditions rather than the freer menotaxes observed in the present experiments.

Our results reported above demonstrate both a menotactic azimuth preference which is parallel to the direction of naturally occurring polarized light in the zenith and the sun's vertical as well as a strong polarotaxis parallel to an imposed e-vector. The correlation observed between these two types of orientation is

suggestive evidence that responses to polarized light may be involved in sun compass orientation by this fish.

SUMMARY

1. Visual orientation of the surface-living hemirhamphid teleost *Zenarchopterus* has been studied with individual fish swimming in an experimental vessel open to the air. Measurements of spontaneous heading preferences were made in the afternoon and morning respectively of two successive days, during which the sun's bearing differed by nearly 180°. Fish were tested under natural illumination of sun and sky as well as with six different *e*-vector directions of imposed linearly polarized light.

2. Data were selected among other things on the criterion that maintenance of a given azimuth direction ± 20° for a 10 sec period counted as an oriented response. Comparison with the distributions of the total measurements justifies this selection.

3. *Zenarchopterus* avoided the azimuth quadrant towards the sun. This suggests negative phototaxis but other explanations are possible.

4. A strong southerly heading preference occurred on both days under natural illumination by sun and sky. The same marked preference is also evident in the with-polarizer data plotted relative to North. This persists in the residual data when the counts are subtracted for the N-S imposed *e*-vector which parallels the sky polarization in the sun's vertical.

5. Such orientation occurred while the sun's bearings were constant; when solar bearings were changing rapidly orientation was less clear or absent. These results support a time compensated sun compass orientation.

6. Responses to imposed polarization patterns show a strong preferential orientation parallel to the *e*-vector. This persists when the N-S imposed *e*-vector counts (which demonstrate strong southerly preferences parallel to the sky polarization in the sun's vertical) are subtracted from the overall data. Comparison with previous underwater experiments on the same species indicates that these water surface data yield stronger polarotaxis and may provide better evidence for normal behavior.

7. The correlation of a menotactic azimuth preference parallel to sky polarization in the sun's vertical with strong polarotaxis parallel to the *e*-vector provided by a polarizer suggests that responses to natural polarized light may be involved in normal direction finding by *Zenarchopterus*.

LITERATURE CITED

BATSCHELET, E., 1965. *Statistical Methods for the Analysis of Problems in Animal Orientation and Certain Biological Rhythms.* American Institute of Biological Sciences Monograph, Washington, 57 pp.

BUDDENBROCK, W. VON, 1917.   Lichtkompassbewegungen bei Insekten, insbesondere den Schmet-
        terlingsraupen.   *Sitzungsberichte der Heidelberger Akademie der Wissenschaften* B,
        8: 1–26.
FRAENKEL, G. S., AND D. L. GUNN, 1940.   *The Orientation of Animals.*   Clarendon Press,
        Oxford, 352 pp.
FRISCH, K. VON, 1950.   Die Sonne als Kompass im Leben der Bienen.   *Experientia,* **6**: 210–221.
HARDEN JONES, F. R., 1968.   *Fish Migration.*   St. Martin's Press, New York, 325 pp.
HASLER, A. D., 1966.   *Underwater Guideposts.*   University of Wisconsin Press, Madison, Wis-
        consin, 155 pp.
IVANOFF, A., AND T. H. WATERMAN, 1958.   Factors, mainly depth and wavelength affecting the
        degree of underwater light polarization.   *J. Mar. Res.,* **16**: 283–307.
JANDER, R., 1963a.   Insect orientation.   *Ann. Rev. Entomol.,* **8**: 95–114.
JANDER, R., 1963b.   Grundleistungen der Licht-und Schwereorientierung von Insekten.   *Z.
        Vergl. Physiol.,* **47**: 381–430.
JANDER, R., 1970.   Ein Ansatz zur modernen Elementarbeschreibung der Orientierungshandlung.
        Z. Tierpsychol., **27**: 771–778.
JERLOV, N. G., 1968.   *Optical Oceanography.*   Elsevier, Amsterdam, 194 pp.
KRAMER, G., 1950.   Orientierte Zugaktivität gekäfigter Singvögel.   *Naturwissenschaften,* **37**:
        188.
KUHN, A., 1919.   *Die Orientierung der Tiere im Raum.*   Fischer, Jena, 71 pp.
LUNDGREN, B., 1971.   On the polarization of daylight in the sea.   *Københavns Universitet,
        Institut for Fysisk Oceanograft,* Report No. **17**: 1–34.
MCCLEAVE, J. D., S. A. ROMMEL, JR. AND C. L. CATHCART, 1971.   Weak electric and magnetic
        fields in fish orientation.   *Ann. New York Acad. Sci.,* **188**: 270–281.
SEKERA, Z., 1957.   Polarization of skylight.   Pages 288–328 in S. Flügge, Ed., *Handbuch der
        Physik,* Vol. XLVIII.   Springer-Verlag, Berlin.
WATERMAN, T. H., 1954.   Polarization patterns in submarine illumination.   *Science,* **120**:
        927–932.
WATERMAN, T. H., 1955.   Polarization of scattered sunlight in deep water.   *Deep Sea Res.,*
        3 Suppl.: 426–434.
WATERMAN, T. H., 1966.   Specific effects of polarized light on organisms.   Pages 155–165 in
        P. L. Altman and D. S. Dittmer, Eds., *Environmental Biology.*   Federation of Amer-
        ican Societies for Experimental Biology, Bethesda, Maryland.
WATERMAN, T. H., 1972.   Visual direction finding by fishes.   In S. R. Galler, K. Schmidt-
        Koenig, G. J. Jacobs and R. E. Belleville, Eds., *Animal Orientation and Navigation,
        A Symposium.*   National Aeronautics and Space Administration, Washington, D. C.,
        in press.
WATERMAN, T. H., AND R. B. FORWARD, JR., 1970.   Field evidence for polarized light sensitiv-
        ity in the fish *Zenarchopterus. Nature,* **288**: 85–87.
WATERMAN, T. H., AND R. B. FORWARD, JR., 1972.   Field demonstration of polarotaxis in the
        fish *Zenarchopterus. J. Exp. Zool.,* **180**: 33–54.